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Selection for maternal behavior in mice—direct and correlated responses

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Abstract

Three generations of divergent selection for a maternal care index (MCI) in mice were practiced in each of three replicates. MCI was recorded for 29–32 dams and litters in each replicate/line subclass. Pups of the top (or bottom) 6–10 dams in each replicate, depending on number of females in the litters, were selected in high (H) and low (L) MCI lines. At birth, litters with more than 10 pups were standardized to 10 pups whereas litters with no more than 10 pups remained intact. On day 4, 8, 12, and 16 of lactation, time budgets during a 30-min session were recorded by real-time video camera. The times spent in the activities of nursing pups, licking pups, retrieving pups, resting with pups, and building a nest were summed, and MCI was the percentage of the total time devoted to these activities. Number born alive (NBA), number weaned (NW), litter weaning weight (LWW), and mating weight (MW) were recorded. The difference between H and L in cumulative selection differential (CSD) of MCI was 59.8%. Regressions of differences in H and L on generation and on cumulative selection differential were 4.878 ± 0.414 and 0.239 ± 0.011 (realized heritability), respectively ($P < 0.01$). Means for MCI in Generation 3 for H and L, respectively, were 80.7 and 63.7% ($P < 0.01$). Variances and covariances among traits were estimated with multiple-trait, derivative-free, restricted maximum likelihood procedures. Estimates of heritabilities of MCI, NBA, NW, LWW, and MW were 0.20, 0.31, 0.12, 0.39, and 0.49, respectively. Genetic correlations of MCI with most traits were low; however, a correlation of 0.78 with number weaned was found indicating selection for MCI may increase pre-weaning survival rate. Selection for MCI was effective because it was heritable (0.24) and highly variable ($CV = 24.8\%$), but changes in MCI were not strongly associated with litter size at birth, litter weaning weight, or dam mating weight.

Keywords: mice, maternal behavior, selection, pre-weaning survival, pre-weaning growth

1. Introduction

Since the 1980s, issues of animal welfare have made study of animal behavior an important part of research in animal production. Some problems in animal production have been found to be associated with abnormal behavior. In swine, pre-weaning piglet mortality, ranging from 7 to around 30%, is still the major loss on many pig farms (Cronin et al., 1996). Piglet mortality is often due to crushing by sows (Cronin, 1985; Spicer et al., 1986; Vaillancourt and Tubbs, 1992; Maderbacher et al., 1993; White et al., 1996). Farrowing crates were introduced in the 1960s to reduce the rate of piglet crushing. Today, this management practice is commonplace in the swine industry. However, focus on animal welfare issues in the 1980s has identified some negative effects, especially in sows' behavior, of the crate confinement system (Cronin and Wiepkema, 1984; Broom, 1986), and some researchers have suggested that farmers not use farrowing crates (Arey, 1993; Phillips and Fraser, 1994).

Considerable research to modify the farrowing environment to ensure sows' welfare has been done, but results vary and are not conclusive (Cronin and van Amerongen, 1991; Cronin and Smith, 1992; Lou and Hurnik, 1994; Cronin et al., 1994; Arey and Sancha, 1996; Cronin et al., 1996).

Since the book *Maternal Behavior in Mammals* (Rheingold, 1963) was published there has been remarkable progress in the study of maternal behavior. Most research focused on causes of maternal behavior and the development of the mother-infant relationship and has already been applied to wildlife conservation and human medicine. From the evolutionary perspective, the function of maternal behavior in pigs should be to minimize neonatal and pre-weaning mortalities. Sellier and Legult (1986) suggested that Chinese breeds, such as Meishan, have higher maternal qualities than the European breeds. In a cross-fostering trial, Van der Steen and de Groot (1992) also found that piglets reared by Meishan sows had higher pre-weaning survival and growth rates than those reared by Dutch Landrace sows. These breed differences suggest that genetic differences in maternal behavior may be related to piglet growth and survival. In a previous study, we used mice as an animal model to test if maternal behavior had a genetic component and found that it did (Chiang et al., 2002). If we can understand more about the inheritance of maternal behavior, selecting good mothers to ensure the welfare of both sows and piglets will be more applicable in the future.

The objectives of this study were to estimate the magnitude of genetic variation of dams' maternal behavior and correlated responses in pups' pre-weaning performance through high and low selection for a maternal care index (MCI). The mouse model was used to evaluate the feasibility of improving pre-weaning survival and growth in piglets through selection for maternal care in sows.

2. Materials and methods

2.2. Animals

The base population came from control lines maintained in another selection project in our laboratory (Nielsen et al., 1997). Two-way divergent selection for three generations

Table 1. Numbers of available litters and litters entering trial (in parentheses)

Line	Generation	Replicate 1	Replicate 2	Replicate 3
High	0	42 (32)	40 (32)	42 (32)
	1	36 (32)	35 (32)	37 (32)
	2	35 (32)	32 (32)	32 (31)
	3	31 (30)	32 (31)	31 (29)
Low	0	42 (32)	42 (32)	41 (32)
	1	36 (32)	36 (32) ^a	36 (32)
	2	36 (32)	35 (32) ^a	36 (32)
	3	34 (31) ^a	35 (32)	36 (32) ^b

^a All pups in one of the litters entering the trial died before the behavior recording began.

^b All pups in two of the litters entering the trial died before the behavior recording began.

was practiced in each of three independent replicates for a total of six unique, closed lines. Replicates were separated in time by 4 weeks. The selection criterion was a MCI.

Numbers of litters in different lines, generations, and replicates are shown in Table 1. The experiment was designed to save 36 female breeders each generation in each line/replicate combination to produce 32 litters per line per replicate in the next generation. However, due to variation in litter sizes and sex ratios, the number of available litters and litters entering the trial varied from replicate to replicate as well as from generation to generation. The first available 32 litters were selected in each line-replicate combination to enter the trial. The generation interval of each replicate was 12 weeks. All litters within each replication/generation were born within 1 week.

2.2. Environment and management

The laboratory was kept at 24 °C with 12 h light to 12 h dark cycles. Besides *ad libitum* access to water, mice in littering cages, which were 15.24 cm × 30.48 cm × 15.24 cm metal cages with 1.27 cm × 1.27 cm metal mesh lids, had *ad libitum* access to a rodent-block diet containing 20% crude protein (CP), 10% fat, and 2% crude fiber. In growing and breeding cages, mice had *ad libitum* access to a rodent-block diet containing 24% CP, 4% fat, and 4.5% fiber. Two to three females were mated to a non-sibling male. Females averaged 9 weeks of age when mated (range of 8.5–9.5 weeks). Each dam was weighed at assignment to a mating cage and mating weight (MW) was recorded. Pregnant mice were transferred to the littering cages individually at the 18th day of gestation. Cages were checked daily for new litters, and the day when the litter was found was assumed to be the day of birth.

In the previous study (Chiang et al., 2002), there was no interaction between lines previously selected for litter size and litter size standardization on MCI ($P = 0.94$), but size of the litter might affect pre-weaning performance, especially pre-weaning survival rate. Thus, litters with more than 10 pups were adjusted to 10 pups at birth and litters with 10 or fewer pups were not adjusted. When adjusting litter size, an ideal sex ratio of three males and seven females was used to save more female pups as breeders for the next generation.

2.3. Maternal care index

On days 4, 8, 12, and 16 of lactation, activities of each dam during one 30 min session that occurred between the times of 09:00–12:00, 12:00–15:00, or 15:00–18:00 h were recorded by real-time video camera. Mice within selection lines were assigned randomly to a time period, with an equal number of mice assigned to each period. Each dam was observed only once on a particular day, however, all dams were observed within each lactation stage and re-randomization of dams to time periods occurred each day. Selection for MCI was based on average MCI across days. In the previous study (Chiang et al., 2002) genetic line by stage of lactation did not affect MCI ($P = 0.56$), although there was an interaction on the time dams spent resting with pups ($P = 0.03$), a trait that was a component of MCI but comprised only 2–5% of the mean. Therefore, even though a circadian rhythm on activity was expected, the procedures of randomly assigning mice to time periods and evaluating mice on four different days was used to avoid bias in selection due to circadian rhythm.

Set-up of video camera and mouse cages was described in Chiang et al., 2002. In a 30-s interval as the videotape was viewed, the recorder took instantaneous observations of behavioral activities of four dams observed simultaneously, and recorded their individual activities using the following behavioral categories (Krackow and Hoeck, 1989): (1) nursing: a dam adopted the lactation position or at least one pup was visibly suckling; (2) licking pups: a dam licked any part of a pup's body; (3) retrieving pups: a dam carried or attempted to carry a pup in the direction of the nest by taking a part of the pup's body into her mouth; (4) nest building: dams transported material toward the nest or manipulated already incorporated material; (5) resting with pups: a dam was inactive and not engaged in any defined behavior and kept contact with a part of her body other than the tail to the body of at least one pup; (6) resting alone: the dam was inactive without contact with any pup; (7) eating and drinking: a dam ingested food or water; (8) grooming: dams were wiping, licking, or scratching their body; and (9) other activities: any activity such as running, sniffing and climbing on bars that was not assigned to one of the above categories. Categories one through five were considered as maternal care. Because each cage was videotaped for 30 min within a 3-h videotaping period, each dam had 60 behavior records for that observation session. The number of times mice were observed performing each activity was summed, divided by 60, and multiplied by 100 to express time observed in each behavior as a percentage. The percentages for the activities in categories 1–5 were summed to calculate the MCI.

2.4. Selection criteria

The average MCI across the four evaluation days was calculated for each dam and used as the selection criterion. The number of litters from which pups were selected as breeders ranged across generations from 6 to 10 in high (H) and 6 to 9 in low (L) MCI lines. The original experimental design was to select the top or bottom 6 of the 32 litters to produce the next generation. However, due to the various sex ratios among litters, more than 6 litters were selected in some generation/replicate combinations to maintain 32 litters for observation. Therefore, the selection intensity varied somewhat across generations.

2.5. Pre-weaning performance data

Number of pups born alive (NBA) was recorded at birth. Number of pups entering the trial (NE) was the number after standardization and was different than NBA in those litters with more than 10 pups born alive. Number of pups (NW) and litter weight (LWW) were recorded at weaning.

2.6. Inter-observer reliability of viewing tapes

During the experiment, one person viewed all videotapes. A post-trial evaluation was performed to investigate the reliability of interpreting the videos. Two additional observers without former experience in behavioral observation were hired to view five randomly selected videotapes that contained 10 h of behavior information. The nine behavior categories were explained in detail before the viewing. Using the same method as that used in the original interpretation, maternal activities were recorded independently by these two observers. These data, along with the original data, were used to evaluate the reliability of interpreting the tapes. Pair-comparison was used. Differences in MCI between the original observer (00) and the first additional observer (A01), between 00 and second additional observer (A02), and between A01 and A02 were analyzed by Proc Means procedure in SAS (SAS, 1997).

2.7. Data analysis

2.7.1. Mean separation

The Proc GLM procedure in SAS (SAS, 1997) was used to generate replication-line-generation subclass least squares means. The model fitted was:

$$Y_{ijkl} = \mu + r_i + l_j + g_k + (rl)_{ij} + (rg)_{ik} + (lg)_{jk} + (rlg)_{ijk} + \beta ne_{ijkl} + e_{ijkl}$$

where Y_{ijkl} is the observation of MCI, NBA, NW, LWW, or MW of mouse i in replicate i , line j , and generation k ; μ the overall mean, r_i the random effect of the i th replicate, l_j the fixed effect of the j th line, g_k the fixed effect of the k th generation, $(rl)_{ij}$ the replication by line interaction, $(rg)_{ik}$ the replication by generation interaction, $(lg)_{jk}$ the line by generation interaction, $(rlg)_{ijk}$ the replication by line by generation interaction, β the slope of regression of Y_{ijkl} on NE, the number in the litter entering the trial (fitted for NW and LWW only), and e_{ijkl} the residual component.

Number in the litter entering the trial (NE) was fitted as a covariate for litter traits at weaning because only litters with more than 10 live pups were adjusted to the same litter size whereas litters with less than 10 pups varied in number nursed.

2.7.2. Evaluation of selection and (co-)variation

Within replicates differences in least squares means between H and L lines were regressed on generation number and on differences in CSD to estimate responses to selection. The regression of MCI on CSD is realized heritability. Replications were a random effect and variance among regressions is the correct variance to assess whether high and low selection lines diverged significantly. Therefore, regressions for each trait were calculated within replication and averaged, and differences between average regressions and

zero were tested with a *t*-test (2 d.f.) for which the denominator was the standard deviation of the within replication regression coefficients divided by the square root of 3.

Cumulative selection differential of the sex-limited trait, as a measure of selection applied, was calculated by the following formula:

$$\text{CSD}_i = 0.5(\text{SDF}_{i-1}) + \sum 0.25(\text{SDF}_{i-2} + \text{SDM}_{i-2}),$$

where SDF is the selection differential of dams, SDM the selection differential of sires through their dams, and *i* denotes the generation number. The SDF in a particular line by replicate combination was calculated by the following formula:

$$\text{SDF}_i = \left[\frac{\sum n_k \text{MCI}_k}{\sum n_k} \right] - \text{MCI}_i,$$

where n_k is the number of daughters of the *k*th dam, MCI_k the maternal care index of the *k*th dam, and MCI_i is the mean of MCI in the *i*th generation. Because MCI could not be recorded in males, selection differential in males was calculated from their dams' records using the following formula:

$$\text{SFM}_i = \left[\frac{\sum n_k \text{MCI}_k}{\sum n_k} \right] - \text{MCI}_i,$$

where n_k is the number of granddaughters through sons of the *k*th dam, MCI_k the maternal care index of the *k*th dam, and MCI_i is the mean of MCI in the *i*th generation.

Multiple-trait derivative-free restricted maximum likelihood (MTDFREML, Boldman et al., 1993) was used to estimate genetic and phenotypic variances and covariances among traits, and heritabilities and genetic and phenotypic correlations. The model fitted in MTDFREML was:

$$Y = X\beta + Z_a a + Z_r r + e$$

where *Y* is the matrix of the observed five traits, β the vector of fixed effects that included the effect of generations, *X* the design matrix that associated records in *Y* with β , *a* the vector of direct additive genetic effects associated with records in *Y* and assumed to have the distribution $a \sim N(0, A\sigma_a^2)$, Z_a the design matrix that associated records in *Y* with *a*, *A* the genetic relationship matrix of observations, σ_a^2 the variance component for animal additive genetic value, *r* the vector of random effects associated with replications, uncorrelated with *a* effects, and assumed to have the distribution $r \sim N(0, I\sigma_r^2)$, Z_r the design matrix that associated records in *Y* with *r*, *I* the identity matrix, σ_r^2 the variance component associated with replications, *e* the vector of residual effects assumed to have the distribution $e \sim N(0, I\sigma_e^2)$, and σ_e^2 is the residual error variance component.

The effect of replicate was fitted as an uncorrelated random effect and the relationship matrix connected animal additive genetic effects as correlated random effects. The five traits MCI, NBA, NW, LWV, and MW were analyzed simultaneously in MTDFREML. Number of pups entering the trial after standardization was fitted as a covariate in the fixed effects for NW and LWV.

Table 2. Differences in maternal care index between observers

	OO–AO1 ^a	OO–AO2 ^b	AO1–AO2 ^c
Difference (%)	–0.0125 ± 0.0671	0.0188 ± 0.0680	0.0313 ± 0.0792

^a The difference in MCI between data recorded by the original observer (OO) and the first additional observer (AO1).

^b The difference in MCI between data recorded by the original observer (OO) and the second additional observer (AO2).

^c The difference in MCI between data recorded by the first and second additional observers (AO1 and AO2, respectively).

3. Results and discussion

Results from comparing the interpretation of the videos are in Table 2. Differences between the original observer and each additional observer and between the two additional observers were small and not significantly different from zero. Thus, we concluded that there was no bias by the original observer in interpreting behavior from the tapes.

Cumulative selection differentials are in Table 3. Similar selection pressure was applied in H and in L lines and selection differentials accumulated uniformly through the three Generations of selection (means for H – L were 21.6, 40.4, and 59.8% in Generations 1, 2, and 3, respectively).

Evolution of MCI and other traits over three generations of selection is illustrated by the least squares means in Table 4. Although, there was some variation in mean MCI across the three Replicates, selection responses were quite similar. In Generation 3, the differences in MCI between the high and low lines in replicates 1, 2, and 3 were 19.2, 17.7, and 14.1%, respectively. No consistent pattern of change between lines H and L in NBA or LWW occurred. However, the trend was for differences between lines in NW to increase and differences in MW to decrease in all replications with increased generations of selection.

Table 3. Cumulative selection differentials for high and low selection lines

Generation	Replicate	Low line	High line	High – low line
1	1	–9.9	10.1	20.0
	2	–11.7	12.1	23.8
	3	–7.5	13.5	21.0
	Average	–9.7	11.9	21.6
2	1	–24.0	20.1	44.2
	2	–21.8	21.0	42.8
	3	–12.0	22.4	34.4
	Average	–19.3	21.2	40.4
3	1	–31.0	26.0	57.0
	2	–35.0	29.6	64.6
	3	–27.4	30.5	57.9
	Average	–31.1	28.7	59.8

Table 4. Least squares means by replication (Rep) and high (H) and low (L) selection lines

Rep	Line	Generation	Maternal care index (%)	Number born alive per litter	Number weaned per litter	Litter weaning weight (g)	Dam mating weight (g)
1	Base	0	64.69	13.38	9.09	NR	NR
	L	1	64.88	11.13	9.20	107.5	24.7
	L	2	76.54	11.17	9.01	101.8	23.8
	L	3	64.14	10.77	9.12	96.6	23.5
	H	1	75.57	11.56	9.48	110.6	23.7
	H	2	79.32	10.81	9.46	107.0	23.7
	H	3	83.36	10.53	9.47	99.9	20.7
2	Base	0	52.18	13.44	9.49	130.3	NR
	L	1	57.01	11.03	9.19	121.4	27.4
	L	2	55.60	11.97	9.24	126.5	28.3
	L	3	56.23	9.77	9.30	113.1	25.1
	H	1	64.61	11.09	9.48	126.8	26.2
	H	2	65.68	10.14	9.49	123.1	26.3
	H	3	73.88	9.77	9.49	106.2	23.0
3	Base	0	70.00	14.19	9.49	143.4	NR
	L	1	75.71	9.60	9.31	114.9	25.4
	L	2	66.27	10.69	9.13	113.0	25.4
	L	3	70.59	10.10	9.23	110.3	24.7
	H	1	83.06	10.47	9.44	110.8	25.2
	H	2	72.39	9.13	9.38	109.9	24.6
	H	3	84.72	8.41	9.41	110.4	23.7

Table 5 contains the regressions of responses on generation number and on cumulative selection differential. The difference in MCI between H and L lines increased at the rate of $4.88 \pm 0.41\%$ per generation. The average realized heritability of MCI, estimated as regression of response on CSD, was 0.24 ± 0.01 ($P < 0.01$). Regressions of responses in NBA and LWW were not significant. However, a correlated positive response in NW of 0.080 ± 0.021 ($P = 0.061$) pups per generation and a negative response in MW of -0.598 ± 0.159 g ($P = 0.064$) occurred. At Generation 3, litters raised by H dams averaged 0.24 pups more than litters by L dams, a difference of approximately 2.3% in pre-weaning survival rate. Mating weight for H dams in Generation 3 averaged across replications was -1.97 g less than for L dams, a decrease of approximately 8.1%.

Estimates of heritabilities and phenotypic standard deviations from the MTDFREML analyses are in Table 6. The estimate of heritability of MCI was 0.20, which is consistent with the realized heritability of 0.24. The heritability of 31% for NBA was higher than expected. Kirby and Nielsen (1993) reported that realized heritabilities in a selection experiment for number born in mice ranged from 0.07 to 0.12. The estimated heritability of NW was 12% and that for LWW was 39%. Mating weight was found to have a heritability of 49%.

The MTDFREML analyses also produced estimates of genetic correlations among traits. The estimated genetic correlation between MCI and NW of 0.78 suggests that se-

Table 5. Regressions (*b*) of differences between high and low selection lines on generation and on cumulative selection differential (CSD), standard errors (SE) of average regressions, and probability (*P*) values for tests of differences of average regressions from zero.

Trait	Replication	Regressions on generation		Regressions on CSD	
		<i>b</i> ± S.E.	<i>P</i> -value	<i>b</i> ± S.E.	<i>P</i> -value
MCI (%)	1	4.975		0.229	
	2	5.542		0.262	
	3	4.118		0.227	
	Average	4.878 ± 0.414	0.007	0.239 ± 0.011	0.002
NBA	1	-0.151		-0.0082	
	2	-0.189		-0.0083	
	3	-0.751		-0.0373	
	Average	-0.364 ± 0.194	0.202	-0.0176 ± 0.0097	0.205
LWW(g)	1	0.090		0.0158	
	2	-2.974		-0.1343	
	3	0.112		0.0071	
	Average	-0.924 ± 1.025	0.462	-0.037 ± 0.049	0.525
NW	1	0.121		0.0066	
	2	0.054		0.0027	
	3	0.065		0.0033	
	Average	0.080 ± 0.021	0.061	0.0042 ± 0.0012	0.075
MW(g)	1	-0.916		-0.039	
	2	-0.444		-0.021	
	3	-0.434		-0.022	
	Average	-0.598 ± 0.159	0.064	-0.0271 ± 0.0057	0.055

lection for MCI will increase pre-weaning survival rate and thus increase number weaned per litter. This finding is consistent with the observed change in NW. The estimated genetic correlation between MCI and MW was -0.19, also consistent with the observed changes between lines H and L across generations. Based on the estimated genetic correlations, selection for MCI will cause little if any change in NBA or LWW. Moderately positive genetic correlations of LWW with NW (0.47) and MW (0.64) were found.

Table 6. MTDFREML estimates of heritabilities (on diagonal), genetic (lower triangle) and phenotypic (upper triangle) correlations among traits, and phenotypic standard deviations (*a*)

Trait ^a	MCI	NBA	NW	LWW	MW	σ
MCI	0.20	-0.10	0.11	-0.03	0.08	17.88%
NBA	-0.20	0.31	-0.05	0.20	0.20	2.00 pups
NW	0.78	-0.01	0.12	0.49	0.04	0.51 pups
LWW	-0.19	0.27	0.47	0.39	0.46	14.66 g
MW	-0.19	0.20	-0.21	0.64	0.49	2.70 g

^a See text for definitions of traits.

In our previous study (Chiang et al., 2002), MCI for unselected and selected litter size lines, which had 12.3 and 15.2 pups per litter, respectively, were $55.0 \pm 1.5\%$ and $64.7 \pm 1.4\%$, respectively. In the current study, the average MCI over four lactation stages of three replicates was around 60%, which was consistent with the previous study.

Behavior was recorded every day over the 21-day lactation period in the previous study, following the method described by Krackow and Hoeck (1989), to get the complete time budget of dams during lactation. In this study, although behavior of dams was recorded only at 4, 8, 12, and 16 day of lactation a similar time budget of dams was found. Therefore, instead of continuous observation, recording at particular time points over the lactation period is an adequate observation method for MCI.

Although divergent selection was practiced in this study, and the selection pressures were quite similar in both directions (Table 3), the selection response of MCI was basically caused by an increase in MCI in the high line. At Generation 3, the average MCI over three replicates in the low lines remained at approximately 60%, which was about the same as in Generation 1, suggesting that mouse dams spend at least, on average, 60% of their time with their pups during the lactation period. In Generations 2 and 3, all pups in four litters in low lines died before the behavior observation began (Table 3). One might surmise that this was due to lack of adequate maternal care. Unfortunately, no data could be collected to support this suggestion. Because no pups could be saved as breeders from these lost litters for the next generation, even though no maternal care was recorded, possible genetic "superiority" for low MCI could not be transmitted to the next generation. This may have also contributed to the lower response in low than in high lines.

Because most research in maternal behavior has focused on application to human medicine, few studies investigating the time budget of maternal behavior in mice were found. One other report, that of Krackow and Hoeck (1989), also reported 60% of dam's time was dedicated to maternal care in mice.

Results from the previous study indicated that selection for larger litter size altered maternal behavior in mice (Chiang et al., 2002). From the results, it was suggested that maternal behavior is influenced by additive genetic variation and that it is genetically correlated with litter size. Therefore, a response in MCI from direct selection and a correlated increase in number born per litter were expected in this study. Part of this expectation was realized as MCI diverged between high and low selection lines at the rate of $4.88 \pm 0.41\%$ per generation. The realized heritability estimates within replications ranged from 0.23 to 0.26 with an average of 0.24 ± 0.01 . However, a positive genetic correlation between MCI and number born per litter was not confirmed. The realized divergence between high and low selection lines was -0.36 ± 0.19 pups per generation. The genetic correlation between MCI and number born per litter was estimated to be -0.20 . Thus, we conclude that maternal behavior as measured by MCI is heritable, but that it has a very low and possibly negative correlation with litter size at birth.

Although, the difference in MCI between high and low lines increased nearly 5% per generation in this three generation selection study, less response in each successive generation was expected because MCI for some dams was nearing the maximum value of 100% in high lines. In Generation 3, mean MCI for high and low lines were approximately 81% and 64%, respectively. If the increasing rate of difference in MCI remained

the same, given that there was no change in MCI for low lines, with four more generations of selection, high line dams would spend all their time with their pups during lactation. From the aspect of evolution and biology, this would not likely happen. To maintain their life and to provide nutritious milk to nurse their pups, dams must spend at least a portion of their time eating and drinking. To take good care of their pups, dams also need to rest for some amount of time. Therefore, with continued selection rate of response would likely decline.

The experimental design was to select the top or bottom 6 of 32 litters in each line to produce the next generation. However, due to variation in sex ratios among litters, selection intensity was adjusted to get enough females to maintain line size. More adjustments of this nature occurred in high than in low lines because sex ratios at weaning shifted in favor of males, although, it had only a small effect on selection differentials. One might speculate that this variation in sex ratios among lines was a chance event, but some evidence exists that it could have been related to the selection criterion. Wilson and Pianka (1963) suggested that parents might be expected to invest more heavily in offspring of one sex. Several investigators have confirmed their suggestion (Dittus, 1979;

Maynard Smith, 1980; Clutton-Brock et al., 1981). When offspring functions differ between males and females, in terms of relative fitness accrued through an offspring to the amount of care that it receives, the sex-biased parental investment is expected. No research was found studying the direct relationship between sex ratio in litters and the amount of maternal care of dams.

Because traits included in MCI are those having to do with interactions of dams and pups, we hypothesized that selection for MCI would increase pre-weaning survival rate of pups. To evaluate the effectiveness of selection on MCI to improve pre-weaning survival rate, the expected selection response for NW from direct selection, selection on MCI, and selection on an index of MCI and NW were calculated following procedures described by Falconer and Mackay (1996) using parameters estimated from MTDFREML. Number weaned per litter after adjustment for number of pups dams were allowed to nurse is equivalent to pre-weaning survival rate, thus this evaluation estimated effects of direct, indirect, and index selection on pre-weaning survival.

Direct selection for NW and selection on MCI were predicted to produce equal responses in NW ($0.061 i$ pups per generation, where i is the standardized selection differential). Index selection for MCI and NW ($I = 0.0031\text{MCI} + 0.1105\text{NW}$) was predicted to increase NW at the rate of $0.083i$ pups, an increase of 36% over selection on either trait alone. The observed response in NW of 0.086 ± 0.036 pups per generation from selection on MCI was consistent with this prediction.

Low genetic correlations of MCI with other traits were found. A negative trend in mating weight occurred, even though the estimated genetic correlation was only -0.19 . The reason is that correlated responses depend on not only the heritability of the directly selected trait and the genetic correlation with the correlated trait, but also on the heritability and phenotypic variation in the correlated trait (Falconer and Mackay, 1996). Mating weight was highly heritable (0.49) and moderately variable ($\text{CV} = 11.7\%$); thus, correlated response in it was relatively large compared with other traits. No similar reports in the literature of relationships between mating weight and behavior were found.

4. Conclusion

Maternal behavior can be altered by artificial selection. The positive genetic correlation between the maternal care index and number weaned per litter, which in standardized litters is equivalent to pre-weaning survival rate, indicates selection for maternal behavior might result in increased pre-weaning survival and increased litter size at weaning. The maternal care index used in this study would not be practical in pigs because of the time and expense of videotaping sows and litters. However, additional study of maternal behavior in pigs is warranted as selection for it might provide an alternative way to improve pre-weaning survival rate of neonatal piglets.

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